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MITIGATING EXOTIC IMPACTS: RESTORING DEER MOUSE POPULATIONS ELEVATED BY AN EXOTIC FOOD SUBSIDY

Dean E. Pearson[1,2,4] and Robert J. Fletcher, Jr.[3,5]

[1]*Rocky Mountain Research Station, USDA Forest Service, Missoula, Montana 59801 USA*
[2]*Division of Biological Sciences, University of Montana, Missoula, Montana 59812 USA*
[3]*Avian Science Center, Division of Biological Sciences, University of Montana, Missoula, Montana 59812 USA*

Abstract. The threat posed by exotic organisms to native systems has led to extensive research on exotic invaders, yet management of invasives has progressed relatively slowly. This is partly due to poor understanding of how exotic species management influences native organisms. To address this shortfall, we experimentally evaluated the efficacy of an invasives management tool for restoring native deer mouse (*Peromyscus maniculatus*) populations elevated by exotic species. The exotic insects, *Urophora* spp., were introduced in North America for biological control of the Eurasian invader, spotted knapweed (*Centaurea maculosa*), but instead of controlling *C. maculosa*, *Urophora* have become an important food resource that doubles *P. maniculatus* populations, with substantial indirect effects on other organisms. We hypothesized that herbicide suppression of *Urophora*'s host plant would reduce the *Urophora* food resource and restore *P. maniculatus* populations to natural levels. Prior to treatment, mouse populations did not differ between controls and treatments, but following treatment, *P. maniculatus* were half as abundant where treatment reduced *Urophora*. *Peromyscus maniculatus* is insensitive to direct herbicide effects, and herbicide-induced habitat changes could not explain the *P. maniculatus* response. Treatment-induced reductions of the *Urophora* food resource offered the most parsimonious explanation for the mouse response. Multistate mark–recapture models indicated that *P. maniculatus* survival declined where *Urophora* were removed, and survival rates were more correlated with variation in population size than movement rates. Other demographic and reproductive parameters (sex ratios, reproductive status, pregnancy rates, and juvenile recruitment) were unaffected by treatment. These results suggest the *Urophora* biocontrol elevated *P. maniculatus* survival, and the herbicide treatment restored mouse populations by removing the exotic food and reducing survival. This work illustrates the importance of mechanistic understandings of community and population ecology for improving invasive species management.

Key words: Centaurea maculosa; *community ecology; demography; exotic species; food limitation; movement;* Peromyscus maniculatus; *population biology; spotted knapweed; survival;* Urophora *spp.*

Introduction

Biological invasions are a leading threat to native species and ecosystems around the world (Wilcove et al. 1998, Mack et al. 2000, Clavero and Garcia-Berthou 2005). Recognition of the magnitude of this threat has stimulated a dramatic increase in research on biological invasions (Smith et al. 2006), but invasive species management has progressed relatively slowly. Recent assessments conclude that advancing management of invasives will require better integration of research and management (D'Antonio et al. 2004, Smith et al. 2006). In particular, there is a need for more rigorous evaluations of management efficacy to better understand the mechanisms determining success or failure of invasive species management tools so that tools can be deployed in the most effective manner. Here, we use recently developed knowledge of the community ecology of an invaded system to apply a management tool for mitigating exotic impacts on a native species. We evaluate the effectiveness of the tool and examine the population-level mechanisms by which it achieves these ends. This study shows how better mechanistic understandings of community and population ecology can improve invasive species management.

Knowledge of the population- and community-level mechanisms underlying exotic–native interactions and their response to management is integral to effective mitigation of invader impacts. For example, classical biological control attempts to reassemble invaded communities based on the community-level understanding that top-down control by the agent will suppress the invader and release native or desirable species (Pearson and Callaway 2003). However, the actual outcome of biological control depends on specific mechanisms at

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[4] E-mail: dpearson@fs.fed.us

[5] Present address: Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611 USA.

both the population and community levels within the system. Biological control is most likely to suppress target weeds when agents attack sensitive life history stages or transitions in the weed's biology (McEvoy and Coombs 1999, Shea et al. 2005). However, whether or not the biocontrol agent succeeds at suppressing the target weed, the response of other nontarget species to biocontrol introductions will depend on community-level interactions (Pearson and Callaway 2005). In some cases, biological control agents effectively suppress their target weeds and release native species (McFadyen 1998, Syrett et al. 2000), but in other cases they may shift the community toward other exotic weeds (Story et al. 2006) or negatively impact native species through a variety of community interactions (Louda et al. 1997, 2003, Stiling and Simberloff 2000, Pearson and Callaway 2003, 2006). These complex outcomes are not restricted to biological control: they can arise from many weed management tools (Zavaleta et al. 2001; Y. K. Ortega and D. E. Pearson, *unpublished manuscript*). Consequently, the likelihood of management mitigating or exacerbating invasive species problems depends on the nature of the systems being managed, the tools being applied, and our knowledge of both.

We apply a weed management tool for mitigating the effects of exotic organisms on native species. The application of this tool was guided by our prior knowledge of the community ecology of a system that has been altered through both the proliferation of an invasive weed and subsequent attempts to control the weed using biological control. Our study system is comprised of the exotic plant spotted knapweed (*Centaurea maculosa*) and two of its exotic insect biological control agents (*Urophora affinis* and *U. quadrifaciata*) that directly and indirectly affect numerous native species. *Centaurea maculosa* is a Eurasian forb that aggressively invades semiarid habitats in western North America (Sheley et al. 1998) and negatively impacts a variety of native plants and animals (Thompson 1996, Ridenour and Callaway 2001, Ortega and Pearson 2005, Ortega et al. 2006; D. E. Pearson, *unpublished manuscript*). A *Centaurea* biological control program was initiated in the early 1970s that has resulted in the introduction of 13 species of exotic insects for *C. maculosa* control (Lang et al. 2000). Despite these efforts, the plant remains extremely abundant where established and continues to spread and increase in new locations (Sheley et al. 1998, Duncan et al. 2004). This failure of top-down control to suppress *C. maculosa* has set the stage for bottom-up effects to expand the impacts of the invasive plant through food web interactions that are facilitated by the exotic biocontrol agents (Pearson and Callaway 2003).

The gall flies *U. affinis* and *U. quadrifaciata* were introduced for spotted knapweed control in the early 1970s (Harris 1980). *Urophora* oviposit within immature *C. maculosa* flowerheads where their larvae induce formation of woody galls that create an energy sink and reduce seed production (Harris 1980). The larvae overwinter within the seed heads from September until June when the adults emerge (Story et al. 1992). Although gall flies reduce *C. maculosa* seed production, they do not suppress *C. maculosa* populations because the plants are not seed limited (Maddox 1982, Stanley 2005). Due to their failure to suppress *C. maculosa*, gall flies have become as abundant as their prolific host and now occur in western North America at densities hundreds to thousands of times greater than in their native range (Myers and Harris 1980).

The superabundance and accessibility of gall fly larvae during winter months has made them a lucrative food resource for generalist native consumers (Story et al. 1995), particularly deer mice (*Peromyscus maniculatus*). Deer mice forage on gall fly larvae from September to June, with *Urophora* comprising 35–50% of their diet in fall and late spring and 85% of their winter diet (Pearson et al. 2000). Observational studies comparing *P. maniculatus* populations where *Urophora* and *C. maculosa* were present with comparable locations where they were absent, found that *P. maniculatus* were more than twice as abundant in the presence of *C. maculosa*. However, this pattern only occurred when *Urophora* were abundant, suggesting that the *Urophora* food resource elevates *P. maniculatus* populations (Ortega et al. 2004, Pearson and Callaway 2006). The mechanism hypothesized for this response was increased overwinter survival given the seasonal availability of the resource, but immigration could not be ruled out as an alternative hypothesis and the causal nature of the *P. maniculatus* response could not be determined in these observational studies.

The bottom-up effects of *Urophora* on *P. maniculatus* may carry over to numerous other native organisms through food-web interactions (Pearson and Callaway 2003). However, the likelihood for such community effects may depend on the demographic mechanisms causing differences in *P. maniculatus* abundance. If patterns of elevated abundances in knapweed-invaded habitats can be explained solely by local immigration from nearby areas, then such local variation in movement may be less likely to have large-scale consequences for population and community dynamics. Alternatively, if survival or reproduction is elevated in the presence of *Urophora* (e.g., through a release from food limitation), this might alter the effective carrying capacities and metapopulation dynamics of *P. maniculatus*. Therefore, experiments designed to quantify the effect of *Urophora* and *C. maculosa* on *P. maniculatus* population size and identify the demographic mechanisms causing variation in population size are needed. Such experiments would provide timely information given recent work suggesting that *Urophora*-associated increases in *P. maniculatus* populations may triple the prevalence of Sin Nombre virus (Pearson and Callaway 2006), the etiological agent for hantavirus pulmonary

syndrome, a disease that is fatal in 38% of human cases (Mills et al. 2002).

Based on previous studies documenting the sensitivity of *C. maculosa* to broadleaf herbicides (Rice and Toney 1998), we hypothesized that broadleaf herbicide treatment would suppress *C. maculosa* and thereby reduce *Urophora*, which are obligate parasites of *C. maculosa*. Reductions in *Urophora* should, in turn, reduce *P. maniculatus* populations and presumably indirect effects associated with elevated *P. maniculatus* populations. We tested this hypothesis in a replicated, large-scale, five-year field experiment using a pre- and post-treatment study design. Our primary objectives were to (1) evaluate whether experimental removal of *C. maculosa* and the *Urophora* food resource reduces *P. maniculatus* populations to pre-invasion conditions and (2) determine the relative role of survival, reproduction, and movement in causing any reductions in *P. maniculatus* populations.

Methods

Study site

The study was located at Calf Creek Wildlife Management Area, approximately 10 km northeast of Hamilton, Montana, in the foothills of the Sapphire Mountains (46°16′ N 114°5′ W). Average annual precipitation is approximately 32 cm, mostly as snow in winter and rain in May and June. Mean monthly minimum and maximum temperatures are 1.6° and 8.6°C during the winter peak in January and 8.6° and 29.3°C during the summer peak in July. The study area is dominated by grassland benches separated by conifer-lined drainages. Study plots were located on the grassy benches where vegetation is generally sparse and the dominant native plants are bluebunch wheatgrass (*Pseudoroegneria spicata*), June grass (*Koeleria macrantha*), and Great Basin sage (*Artemisia tridentata*). *Centaurea maculosa* has become the dominant plant since invading the study site in the 1970s. Domestic grazing has been excluded at Calf Creek since 1960.

Overall experimental design

Sampling was conducted from 1999 to 2003 on four replicate plots. Plots were selected for homogeneous vegetation, microtopography, and soil conditions and were spaced $\geq$500 m apart. Each plot was comprised of three parallel transects 220 m long and 50 m apart running perpendicular to the slope. One sampling station was located every 10 m along each transect totaling 22 sampling stations per transect. On 5 May 2000, *C. maculosa* and *Urophora* were removed from half of each plot by helicopter spraying the broadleaf herbicide Tordon (Dow Agrosciences LLC, Indianapolis, Indiana, USA) at 1.24 L/ha. Herbicide treatment was randomly assigned to half of each plot, splitting transects in half. This design was implemented to explicitly test for the influence of the *Urophora* food resource on reproduction, survival, and local movements. Treatments covered tens of hectares resulting in large buffer strips on the three exposed sides of each treated plot (buffers were >500 m on all sides of all but one plot where the buffer ranged from approximately 50 m on one side to 200 m on the other two sides). *Centaurea maculosa* is very sensitive to Tordon allowing the treatment to target *C. maculosa* and minimize impacts on native plants (Rice and Toney 1998). As obligate parasites, *Urophora* are eliminated with their host plant.

Within each plot, we monitored potential changes in vegetation cover, *Urophora* and other invertebrate foods, and *P. maniculatus*. Vegetation cover was monitored to evaluate whether the treatments effectively reduced *C. maculosa*, quantify habitat changes, and determine to what extent vegetation structure might be responsible for the *P. maniculatus* response. Abundance of *Urophora* and other invertebrates was monitored to understand the potential changes in food resources for *P. maniculatus*. Finally, *P. maniculatus* was monitored using mark–recapture techniques to estimate changes in population size, survival, movement, and reproduction.

Vegetation, Urophora, and other invertebrate sampling

Percent cover of *C. maculosa*, other forbs, grasses, and shrubs were visually estimated over a 5 m radius circular plot centered on each sampling station during the first week in July 1999–2003. *Urophora* larvae were quantified in 1999 and 2000 as the number of larvae per *C. maculosa* seed head by haphazardly collecting 10 seed heads from within 1 m of each sampling station in the fall and dissecting the seed heads to count the larvae within. In 2001 and 2002, *Urophora* were quantified in 0.5-m^2 quadrats placed 0.5 m uphill from each sampling station. Within each frame, percent cover of *C. maculosa* was estimated and the number of *C. maculosa* stems and seed heads were counted. A random subset of 20 seed heads was selected from each station to quantify the larvae within. These data were used to calculate the density of larvae per seed head and per 0.5 m^2 in 2001 and 2002 and to determine the relationship between *C. maculosa* cover, *C. maculosa* seed heads, and *Urophora* larvae for extrapolating larval densities over all years (see *Analyses*). *Urophora* were not quantified in 2003 since this cohort would not provide food for mice until after the study ended. To quantify possible effects of treatment on other potential food resources, we conducted pitfall sampling for invertebrates, which are the dominant food for *P. maniculatus* in semiarid grasslands in this region (Johnson 1961, Pearson et al. 2000). Pitfalls were 355-mL cups containing 120 mL of formalin placed in the bottom of 2-L plastic soda bottles with the tops cut off and inverted to form funnels that directed captures into the cups. We placed pitfalls at the center of every third sampling station (30-m intervals) starting 30 m from the treatment boundary so that there were six pitfalls on each transect (three on each side of the treatment boundary). We conducted pitfall sampling

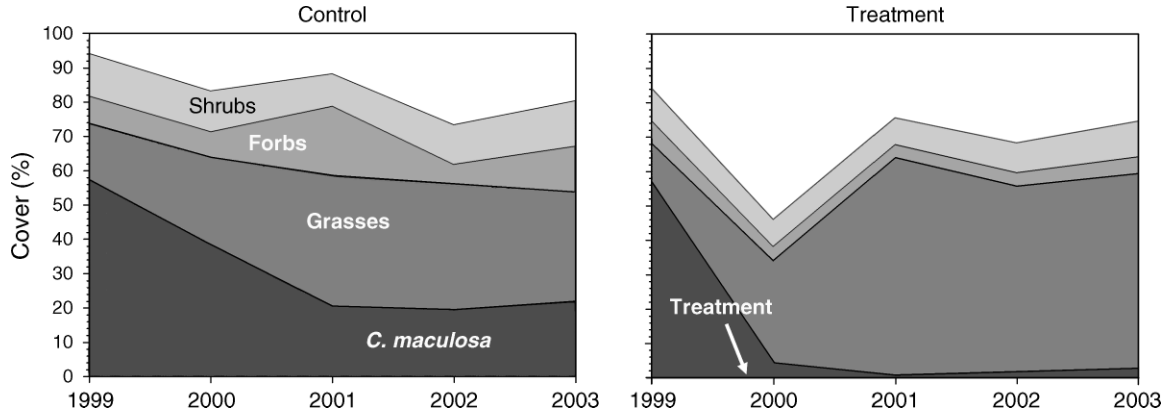

FIG. 1. Changes in vegetation cover including total cover (top line), shrubs, grasses, *Centaurea maculosa* (invasive spotted knapweed), and forbs other than *C. maculosa*, on untreated control plots vs. herbicide-treated plots, 1999–2003.

over three three-week periods in spring, summer, and fall, 2000–2003, concurrent with mouse trapping (see *Deer mouse sampling*), so that sampling began one week before and ended one week after each trapping session. Invertebrates were identified to order and counted. We focused our analysis on Orthoptera, Lepidoptera, Coleoptera, and Arachnida, because other work at this study site indicated that, aside from *Urophora*, these orders dominate the *P. maniculatus* diet (D. E. Pearson, *unpublished data*).

Deer mouse sampling

We sampled *P. maniculatus* populations using Sherman folding live traps (7.6 × 8.9 × 22.9 cm; H. B. Sherman Traps, Tallahassee, Florida, USA). Traps were spaced at 10-m intervals along the three transects on each replicate plot. This resulted in 22 trap stations per transect with 11 stations on each side of the treatment boundary, beginning 10 m from the boundary. We ran one trap at each sampling station for four days. We baited traps with peanut butter and whole oats, and we covered traps with closed cell foam and placed polypropylene batting inside to protect mice from inclement weather. Trapping was conducted in spring (last week in April), summer (first week in July), and fall (first week in October). We checked traps each day before 11:00 hours, and captured animals were identified to species and tagged with uniquely numbered 1005-1 monel ear tags (National Band and Tag Company, Newport, Kentucky, USA). We determined the sex, mass, and reproductive status of each individual prior to release at the trap station. *Peromyscus maniculatus* were weighed to the nearest 0.5 g and age was assigned based on pelage as juvenile (all gray), subadult (mottled gray-brown), or adult (all brown or beginning adult molt). Females were deemed reproductively active if visibly pregnant or if mamma were visibly swollen. Males were deemed reproductively active if testes were palpable or fully descended. We also snap trapped mice during all live trapping periods for diet analysis (results not reported here). Snap trap lines of six standard snap traps baited with peanut butter were set out at 40-m intervals along two transects centered between the three live trap transects (25 m from either live trap transect) for a total of 12 snap traps per plot, six on either side of the treatment boundary. We checked snap traps along with live traps during each four-day sampling period. Plots and treatments were sampled simultaneously during each trapping period.

Analyses

This experiment was designed to test for two a priori explanatory variables that could influence *Peromyscus* populations: treatment and season. Season was considered important because *P. maniculatus* predation on *Urophora* changes seasonally (Pearson et al. 2000). We also considered year effects in the analyses, focusing on how a drought in spring of 2000 that substantially reduced the *Urophora* resource on control plots (see *Results*) potentially influenced *Peromyscus* populations.

We estimated *P. maniculatus* abundance and associated variance for each four-day trapping interval for each control and treatment plot by considering the population closed within each season (Otis et al. 1978) using Program MARK (White and Burnham 1999). Population abundance was estimated using the jackknife estimator (Model M_h; Otis et al. 1978), which incorporates individual heterogeneity into capture probabilities. Estimates were analyzed using generalized linear mixed models for count data (i.e., Poisson regression; PROC GLIMMIX [SAS Institute 2003]) in a repeated-measures framework where treatment, season, and year were fixed factors.

We used a multistate mark–recapture approach (Schwarz et al. 1993) to estimate the influence of *Urophora* food subsidy removal on the survival and movement of *P. maniculatus*. Each four-day trapping period was collapsed to a single capture event (15 total

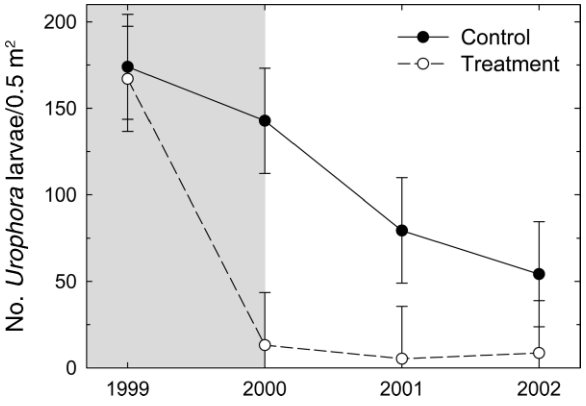

FIG. 2. Change in larval densities (mean ± SE) of exotic gall flies *Urophora* spp. on untreated control and herbicide-treated plots from 1999 to 2002. *Urophora* abundance was not estimated in 2003, because *Urophora* produced in 2003 provide food for mice beginning in fall 2003, after the study ended. Pretreatment sampling periods are shaded in gray.

capture events; spring, summer, fall, 1999–2003). For each event, we assigned each animal to control or treatment based on where it was captured most during the four-day period. Animals captured an equal number of times on both sides of the treatment boundary within a four-day period were removed from the analysis (2% of total individuals), resulting in 1312 individuals used in the analysis. Capture histories were then tallied across the 15 capture intervals. Survival (S) was estimated by partitioning apparent survival (ϕ) from the probability of movement (ψ) between treatment and control areas. For example, survival during time period i in treatment areas (t) can be described as $S_i^t = \phi_i^t/\psi_i^{tc}$, where c is the control. Snap and live trap mortalities were incorporated into the population modeling to account for animals removed (White and Burnham 1999). Because there were no estimable differences between *C. maculosa*, *Urophora* food subsidies, or mice on control and treatment plots prior to treatment (Figs. 1, 2, 4), and treatments were randomly assigned, we pooled pretreatment plots to reduce the number of parameters estimated. Treatment was considered to first potentially influence survival and movement during winter 2000–2001, because *Urophora* produced in the summer provide food for mice beginning in fall (Pearson et al. 2000).

We used a modified step-down approach to develop the most parsimonious model for explaining survival and movement of *P. maniculatus* (Lebreton et al. 1992, Tallmon et al. 2003). We began with a global model that included treatment, season, year, and their interactions (trt × seas × year) for each parameter. We first varied the parameter of least interest, the capture probability, p, comparing the global model to reduced models. Next, we varied movement, and finally survival. In each step, we removed year, then season, and then treatment to reflect our a priori expectations (as described above). We tested the fit of the global model by estimating the overdispersion parameter, $\hat{c}$, using the median $\hat{c}$ procedure in MARK. Models were compared using AIC_c (AIC, adjusted for sample size) and AIC_c model weights (likelihood of a model relative to other models considered [Burnham and Anderson 1998]) in MARK (Burnham and Anderson 1998, White and Burnham 1999).

We evaluated the response of other demographic and individual fitness components to *Urophora* removal, including sex ratios, reproductive activity, juvenile recruitment, and body mass, separately using mixed linear models in PROC MIXED that compared indices of each population parameter over time with plot as a random blocking factor and treatment, year, and season as fixed factors in a repeated-measures framework (SAS Institute 2003). We combined adults and subadults for sex ratios and reproduction indices to distinguish potential breeders from non-breeding juveniles. We calculated sex ratios as the proportion of adult and

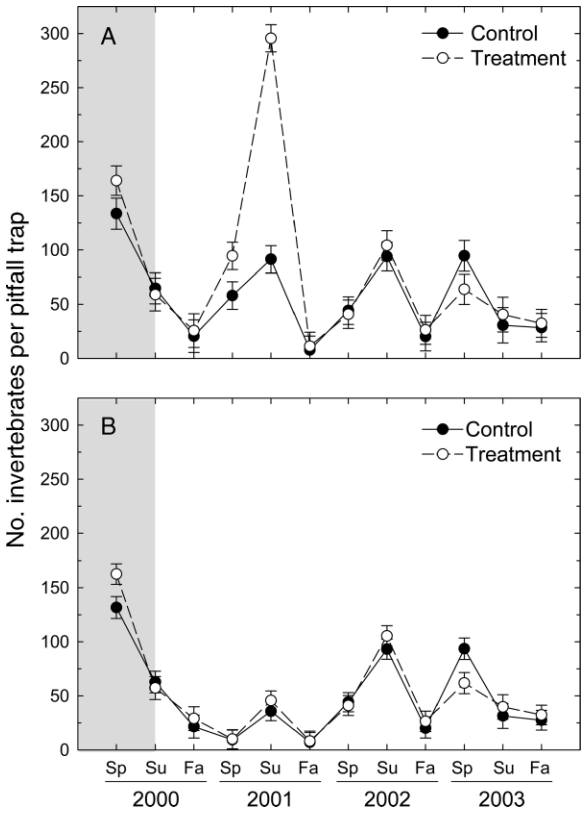

FIG. 3. Abundance of *Peromyscus maniculatus* invertebrate foods captured in pitfalls. Data are pooled from the four orders that dominate deer mouse stomachs in this area: Orthoptera, Lepidoptera, Coleoptera, and Arachnida (all four orders showed a similar pattern). The spike in panel A is due to the biocontrol agent weevils *Larinus* spp. dispersing in search of their host plant *C. maculosa* that was removed by treatment. Panel B shows the same data without the biocontrol weevils. Pretreatment sampling periods are shaded in gray. Abbreviations are: Sp, spring; Su, summer; Fa, fall.

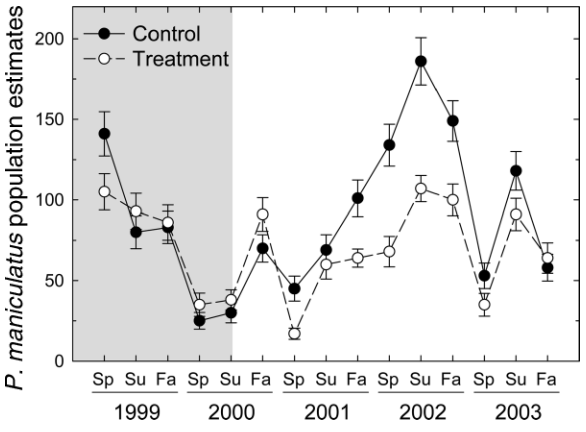

FIG. 4. Population estimates (±SE) for *P. maniculatus* from spring 1999 through fall 2003 on control plots with *Urophora* winter food subsidies present and treatment plots where food subsidies were removed by herbicide treatment of the host plant. Treatment occurred in May 2000 but was expected to first influence mice in spring of 2001 because mice forage on *Urophora* over winter. Pretreatment sampling periods are shaded in gray. Abbreviations are: Sp, spring; Su, summer; Fa, fall.

subadult males to adult and subadult females. Reproductive activity was defined separately for males and females as the ratio of reproductively active adults and subadults to total adults and subadults. Pregnancy rate was the ratio of visibly pregnant adult and subadult females to all adult and subadult females. Juvenile recruitment was the ratio of juveniles to adult and subadult females. Body mass was indexed only for adult males using mass at first capture (Pearson et al. 2003).

To identify potential causal mechanisms for the *P. maniculatus* response to treatment, we tested for effects of treatment and year on estimates of vegetation cover, *Urophora* density, and relative abundance of other invertebrate foods. We compared total vegetation cover by treatment and over time using mixed linear models (PROC MIXED) with treatment as a fixed factor, plot as a random blocking factor, and year as a repeated measure (SAS Institute 1999). Pretreatment total cover was entered as a covariate to control for initial cover differences. We compared *Urophora* density by treatment and over time in the same manner as for total vegetation cover. To estimate *Urophora* densities per 0.5 m^2, we first estimated *C. maculosa* percent cover per 0.5 m^2 over all years based on the linear regression between *C. maculosa* cover estimated over 78.5-m^2 plots (5 m radius) and nested 0.5-m^2 plots from 2001–2002 when both methods were used ($R^2 = 0.48$, $F_{1,525} = 444.47$, $P < 0.001$). We then used linear regression to estimate seed head densities from *C. maculosa* cover from 0.5-m^2 plots from 2001–2002 when these relationships were directly measured ($R^2 = 0.43$, $F_{1,526} = 395.86$, $P < 0.001$). Data were combined from both years for the regressions to incorporate interannual variation. *Urophora* densities were then calculated as $y = (mx + b)u$; where y = *Urophora* density, $m = 1.948$, $x = C.$ *maculosa* percent cover, $b = 6.492$, and $u =$ mean *Urophora* density per seed head as estimated from seed head dissections for each station in each year (m is the coefficient and b is the constant from the regression equation between *C. maculosa* cover and seed heads). Abundance of invertebrates from pitfalls was compared by treatment and over time using PROC MIXED with treatment as a fixed factor, plot as a random blocking factor, and year as a repeated measure. The four invertebrate orders were pooled for analyses because patterns were similar among orders.

RESULTS

Vegetation, Urophora, and invertebrate response

Total vegetation cover did not differ overall by treatment ($F_{1,5} = 1.21$, $P = 0.321$), but it did differ over time ($F_{3,15} = 7.20$, $P = 0.003$) and over time by treatment ($F_{3,15} = 54.73$, $P < 0.016$; Fig. 1). The significant interaction between treatment and year was due to a reduction in total vegetation cover in 2000 on the treatment plots that resulted from the removal of *C. maculosa* by the herbicide (the only significant treatment by year contrast was 2000; $F_{1,14} = 14.31$, $P < 0.002$). However, grasses compensated by 2001, so that total cover was comparable on treatment and control plots relative to pretreatment conditions overall. On herbicide-treated plots, *C. maculosa* declined from 57.3% to 0.4% cover by 2001 (Fig. 1). Unfortunately, *C. maculosa* on control plots declined concurrent with the herbicide treatment from 57.4% to 20.5% by 2001. The decline in *C. maculosa* cover on control plots was negatively correlated with prior June precipitation over the five-year period ($R^2 = 0.761$, $F_{1,3} = 9.576$, $P = 0.054$) suggesting that acute spring drought conditions caused this decline; an observation corroborated by other studies in the region (Ortega et al. 2004, Stanley 2005). *Urophora* densities declined in response to drought and treatment in a manner similar to *C. maculosa* (Fig. 2). *Urophora* densities differed among years ($F_{2,11} = 7.57$, $P = 0.009$) between treatments ($F_{1,5} = 54.65$, $P < 0.001$) and between treatments by year ($F_{2,11} = 5.66$, $P = 0.022$). Thus, despite the drought, the herbicide treatment reduced *Urophora* densities on removal plots to 7% of that on controls by 2001. Abundance of invertebrates captured in pitfalls fluctuated similarly over time on control and removal plots except for a brief spike in invertebrate abundance on removal plots in the spring and summer of 2001 (Fig. 3A). This spike resulted from other *C. maculosa* biological control agents, knapweed flower weevils (*Larinus* spp.), appearing in high numbers in removal plot pitfalls as they emerged in spring and summer without host plants. Excluding the weevils, invertebrate abundance differed by year ($F_{3,32} = 16.29$, $P < 0.001$) and by season ($F_{2,67} = 13.88$, $P < 0.001$) , but not by treatment ($F_{1,24} = 0.44$, $P = 0.511$), treatment by year ($F_{3,31} = 0.32$, $P = 0.807$), or treatment by season ($F_{2,67} = 0.23$, $P = 0.793$; Fig. 3B).

TABLE 1. Candidate set of multistate mark–recapture models for estimating survival and movement of *Peromyscus maniculatus* relative to season, treatment, and year, 1999–2003.

Model	AIC_c	ΔAIC_c	w_i	K
Capture estimation:				
S(trt×seas×yr)ψ(trt×seas×yr)p(trt×seas×yr)	1834.7	0.0	0.77	52
S(trt×seas×yr)ψ(trt×seas×yr)p(trt×seas)	1839.7	5.0	0.06	45
S(trt×seas×yr)ψ(trt×seas×yr)p(seas)	1840.3	5.6	0.05	43
S(trt×seas×yr)ψ(trt×seas×yr)p(.)	1842.0	7.2	0.02	44
Movement estimation:				
S(trt×seas×yr)ψ(trt×seas+yr)p(trt×seas×yr)	1842.4	7.7	0.02	46
S(trt×seas×yr)ψ(trt×seas)p(trt×seas×yr)	1853.2	18.4	0.00	43
S(trt×seas×yr)ψ(trt+seas)p(trt×seas×yr)	1851.2	16.5	0.00	42
S(trt×seas×yr)ψ(trt)p(trt×seas×yr)	1847.5	12.8	0.00	40
S(trt×seas×yr)ψ(seas)p(trt×seas×yr)	1851.8	17.1	0.00	41
S(trt×seas×yr)ψ(.)p(trt×seas×yr)	1848.3	13.6	0.00	39
Survival estimation:				
S(trt×seas+yr)ψ(trt×seas×yr)p(trt×seas×yr)	1845.1	10.4	0.00	43
S(trt×seas)ψ(trt×seas×yr)p(trt×seas×yr)	1847.4	12.7	0.00	39
S(trt+seas)ψ(trt×seas×yr)p(trt×seas×yr)	1843.8	9.1	0.01	37
S(trt)ψ(trt×seas×yr)p(trt×seas×yr)	1843.4	8.7	0.01	35
S(seas)ψ(trt×seas×yr)p(trt×seas×yr)	1843.8	9.0	0.01	36
S(.)ψ(trt×seas×yr)p(trt×seas×yr)	1846.6	11.9	0.00	35

Notes: AIC_c is the Akaike information criterion corrected for sample size. ΔAIC_c compares each model to the model with the lowest AIC_c. AIC_c weight (w_i) indicates the relative likelihood of the model for the given data, compared to other models considered. K indicates the number of parameters in the model. Abbreviations are: S, survival; ψ, movement; p, capture probability; trt, treatment; seas, season; yr, year.

Deer mouse response

Peromyscus maniculatus dominated the small mammal community, comprising 98% of all captures. Thus, it was unlikely that interspecific interactions among small mammals confounded treatment response. Despite fluctuations among years ($F_{4,55} = 23.60$, $P < 0.001$) and seasons ($F_{2,55} = 14.27$, $P < 0.001$), *P. maniculatus* populations were significantly more abundant on subsidized control plots (nearly two times more abundant on average) than on unsubsidized removal plots following treatment ($F_{1,3} = 12.74$, $P = 0.038$; Fig. 4). Season by treatment was not significant, nor was year by treatment ($F_{2,55} < 0.88$, $P > 0.42$).

For the survival and movement analysis, estimation of the overdispersion parameter indicated the global mark–recapture model fit the data relatively well ($\hat{c} = 1.30$). Overall, the most complex model was strongly supported based on AIC_c and model weights (Table 1). The most complex model included interactions of treatment, season, and year on survival, movement, and capture probability of mice. Estimates from this model suggest that survival was variable (as expected from a complex model), but on controls survival tended to be similar to, or higher than that on treatments, except for the first year following the treatment (Fig. 5), with average survival on treatments being approximately 38% less than on controls after treatment. Movement was more variable, with movement from treatments to controls being greater during the winter of 2001 through the fall of 2002, whereas the reverse occurred during other time periods. Correlations of survival and movement estimates with population estimates of *P. maniculatus* indicate that survival, not movement into or out of plots, better explained variation in population abundance (Fig. 6). The weak effect of movement is largely attributable to the fact that only 4% of animals moved across the treatment boundary.

Demographic and fitness measures tended to differ by year and season (Fig. 7). Proportions of reproductive males, reproductive females, proportion of pregnant females, and juvenile recruitment rates differed by year (F values < 2.40, $P \leq 0.05$) and by season (F values > 4.40, $P < 0.02$). Sex ratios did not differ by season or year (F values < 2.00, $P > 0.13$). These patterns reflected seasonal and annual variation expected for a seasonally breeding temperate zone small mammal. Overall, there was no evidence that treatment altered sex ratios or any measure of reproductive allocation or output, including the proportion of reproductively active males and females, the proportion of pregnant females, or juvenile recruitment (F values < 2.00, $P \geq 0.12$; Fig. 7). Body mass differed by season ($F_{2,73} = 16.06$, $P < 0.001$), but not by treatment ($F_{1,32} = 0.23$, $P = 0.633$), or year ($F_{4,45} = 0.84$, $P = 0.505$). Spearman rank correlations indicated that proportion of reproductive males ($r_S = -0.44$, $P = 0.02$), proportion of reproductive females ($r_S = -0.23$, $P = 0.23$), proportion of pregnant females ($r_S = -0.10$, $P = 0.60$), and body mass of adult males ($r_S = -0.37$, $P = 0.04$) tended to be negatively correlated with *P. maniculatus* population estimates, but only the proportion of reproductive males and adult male body mass were significantly correlated. Sex ratios ($r_S = 0.19$, $P = 0.31$) and juvenile recruitment ($r_S = 0.29$, $P = 0.12$) were weakly positively correlated with population estimates, but not significantly so.

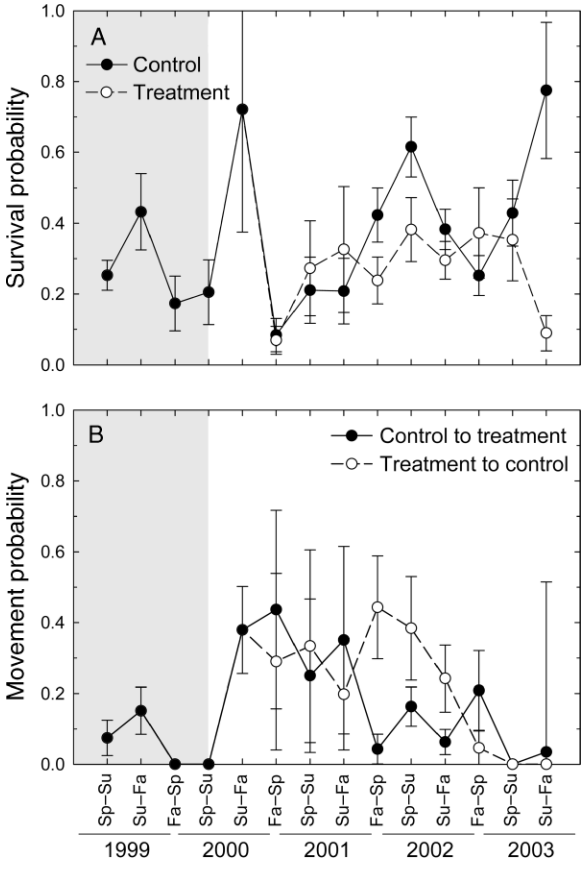

FIG. 5. Estimates (mean ± SE) of *P. maniculatus* survival and movement probabilities over time on control plots where the *Urophora* food subsidy was present and on treatment plots where the food subsidy was removed. Survival probabilities are estimated from spring to summer (Sp–Su), summer to fall (Su–Fa), and fall to spring (Fa–Sp). Prior to treatment, control and treatment plots were assumed similar to reduce the number of estimated parameters (see *Methods*). Treatment occurred in May 2000. Pretreatment sampling periods are shaded in gray.

Although treatment did not change abundance of natural invertebrate food resources or total vegetation cover, there was a shift in vegetation subclasses that might explain the *P. maniculatus* response to treatment. To evaluate this, we conducted a multiple regression of vegetation cover subclasses (arc-transformed percent cover *C. maculosa*, grass, forb, shrub, and other) on *P. maniculatus* population estimates separately for each season using PROC GLIMMIX assuming a Poisson distribution and treating year as a repeated measure. Results indicated no significant relationships between any cover classes and *P. maniculatus* populations except in spring when *C. maculosa* cover was positively correlated with mouse abundance ($F_{1,27} = 23.42$, $P < 0.001$).

DISCUSSION

Efficacy of treatment for restoring mouse populations

Incomplete or inaccurate knowledge of management tools and the systems they are applied in can sometimes exacerbate rather than mitigate impacts of exotic species. *Urophora* introductions were intended to mitigate invader impacts by reducing *C. maculosa* populations, but instead they appear to elevate populations of a native generalist consumer (Fig. 4; Ortega et al. 2004, Pearson and Callaway 2006), thereby expanding the impact of the original exotic invader through food-web interactions. For example, *Urophora* introductions have

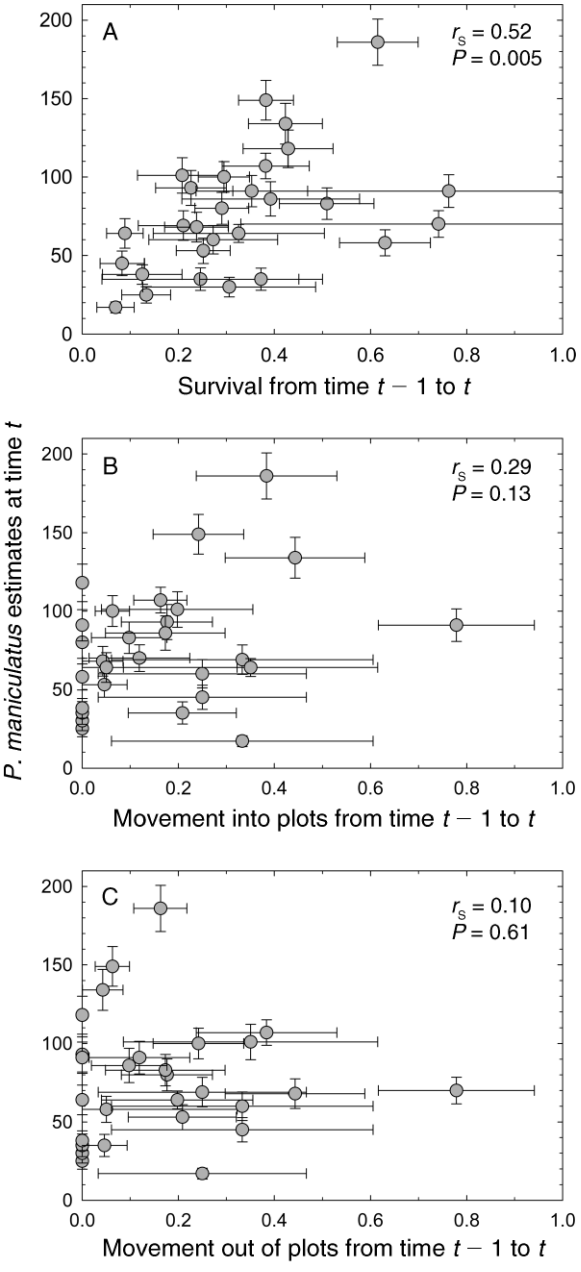

FIG. 6. Spearman rank correlations of population estimates (mean ± SE) for *P. maniculatus* with (A) survival and (B) movement into and (C) movement out of plots (i.e., immigration and emigration) estimated from the most parsimonious multistate mark–recapture model (the model with the lowest AIC_c; Table 1).

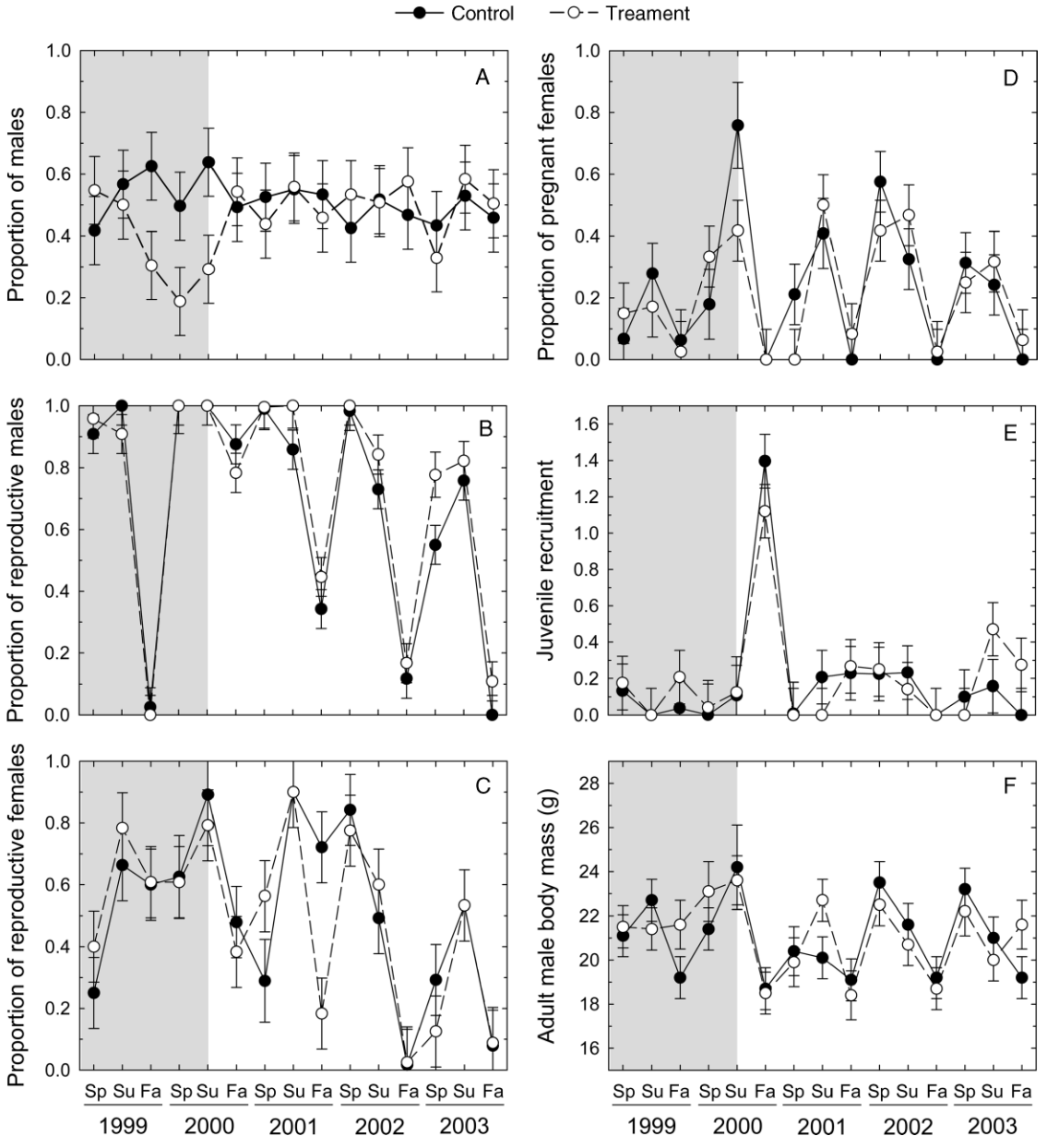

FIG. 7. Estimates (mean ± SE) of *P. maniculatus* demographic and fitness parameters for control plots vs. treatment plots where *Urophora* and *C. maculosa* were removed. Pretreatment sampling periods are shaded in gray. Abbreviations are: Sp, spring; Su, summer; Fa, fall.

been linked to an increase in *P. maniculatus* predation on native plant seeds (D. E. Pearson and R. M. Callaway, *unpublished data*) and an increase in Sin Nombre virus, the etiologic agent for hantavirus pulmonary syndrome in humans (Pearson and Callaway 2006). As a result, *C. maculosa* invasions are now more problematic than before *Urophora* were introduced for biological control.

In an effort to alleviate these impacts, we applied a broadleaf herbicide to kill *C. maculosa* and remove the exotic *Urophora* food resource. The herbicide treatments reduced *P. maniculatus* populations by nearly 50% on treatment relative to control plots for >2.5 years following treatment. This outcome was consistent with expectations based on prior research. Previous studies showed that *P. maniculatus* populations were on average approximately two times more abundant in *C. maculosa*-invaded habitats than comparable native habitats independent of local mouse densities (Ortega et al. 2004, Pearson and Callaway 2006). This suggests that

the 50% decline in mouse populations we observed on treatment plots approximates natural mouse densities for our study areas, i.e., the treatment successfully restored mouse populations to natural densities. We expect this reduction in mouse populations should translate to a reduction in exotic impacts that are transmitted as indirect effects through mice (Pearson and Callaway 2003). For example, although we did not measure Sin Nombre virus levels in *P. maniculatus* populations in this study; prior work indicates this is primarily a density-driven response that should dissipate as mouse density normalizes (Pearson and Callaway 2006).

Potential causes for treatment response

Although in this study the treatment restored *P. maniculatus* populations to normal levels as intended, simply documenting this success does not ensure the repeatability of this outcome. To achieve consistent results with a management tool, it is necessary to understand how the tool works. Potential explanations for the observed response of mice to the treatment include (1) direct effects of herbicide on mouse populations, (2) indirect effects of herbicide on mice through habitat alterations, and (3) indirect effects of herbicide on mice through changes in food resources. While we did not test for direct effects of herbicide on mouse populations, studies examining herbicide effects on *P. maniculatus* populations have found no evidence for direct impacts on survival, reproduction, recruitment or growth in this species (Sullivan and Sullivan 1981, Sullivan 1990, Sullivan et al. 1998).

As with many management actions, herbicides can affect small-mammal populations by altering the vegetation that provides their habitat. Small mammals often respond to herbicide-induced reductions in vegetation cover in proportion to the vegetation response and in a direction consistent with their habitat needs (see Sullivan et al. 1998 and discussions therein). *P. maniculatus* generally respond positively to disturbance (Pearson 1999), and these mice increase following disturbances that reduce vegetative cover in western grasslands (Grant et al. 1982, Rosenstock 1996). In this study, total vegetation cover on treatment plots decreased somewhat following treatment in 2000, but mice showed no response to treatment during this year (Figs. 1 and 4). Although total vegetative cover did not differ significantly after 2000, it tended to be lower on the treatment following the herbicide-induced disturbance. If *P. maniculatus* response following treatment was due to changes in vegetation cover, we would expect that mouse populations should either increase or remain stable on treatment plots, but mice declined instead. Moreover, *P. maniculatus* abundance showed no response to specific cover classes except in spring when it was positively associated with *C. maculosa*. The fact that this positive association with *C. maculosa* occurred only in spring, a period of high *Urophora* foraging, and not in summer, when *Urophora* are absent from *C. maculosa,* or early fall, when mouse foraging on *Urophora* is just beginning, suggests this response is driven by the *Urophora* food resource and not the plant as a habitat feature. Although habitat changes could potentially affect *P. maniculatus* survival by interfering with mouse predators, there is little evidence for this sort of interaction. A large-scale, replicated study excluding avian and mammalian predators in nearby grasslands shows no indication that *P. maniculatus* populations are suppressed by predation after four years of predator exclusion (J. L. Maron and D. E. Pearson, *unpublished data*). A similar study in the northeastern United States has shown no population release in the congeneric *Peromyscus leucopus* following predator exclusion (Yunger 2004). Thus, changes in vegetation are unlikely to have released mice from predation effects and mice showed little response to general vegetation changes associated with treatment.

Although, *P. maniculatus* populations may not be predator limited, this species does respond positively to experimental food addition (Gilbert and Krebs 1981, Taitt 1981, Morrison and Hall 1998), and *Peromyscus* populations are elevated by environmental conditions that increase food resources (Jones et al. 1998, Yates et al. 2002). In this system, *P. maniculatus* eat seeds when available, but invertebrate prey dominate their diet for most of the year (Johnson 1961, Pearson et al. 2000). Forbs that produce the larger seeds consumed by mice in this system (e.g., *Balsamorhiza sagittata*, *Lupinus* spp., and *Lithospermum* spp.) were negligible on our study sites ($<5\%$ of total vegetation), and the treatment did not alter abundance of invertebrates other than *Urophora* (Figs. 2 and 3). Habitat studies show that *P. maniculatus* select strongly for *C. maculosa* when actively feeding on larvae but actually avoid the plant when larvae are absent (Pearson et al. 2000, Ortega et al. 2004). Observational studies also indicate that *P. maniculatus* are more abundant in *C. maculosa* invaded grasslands, but only when *Urophora* are abundant (Ortega et al. 2004, Pearson and Callaway 2006). These studies suggest that *P. maniculatus* associates with *C. maculosa* only to forage on *Urophora* larvae. Thus, although we could not completely isolate the *Urophora* effect on mice from other potential effects of herbicide, the treatment-induced decline in the *Urophora* food resource offers the most parsimonious explanation for the observed decline in *P. maniculatus* populations. These results suggest that *P. maniculatus* are food-limited in this system and that the exotic biocontrol agents provide a superabundant food resource that elevates their populations. Herbicide applications appeared to reduce *P. maniculatus* populations by reducing the exotic food resource, but the overall importance of this treatment depends on whether the underlying population mechanisms involve *in situ* changes in reproduction or survival or local redistribution of mice through changes in immigration and emigration.

Mechanisms underlying changes in mouse populations

Evaluation of mechanisms potentially causing the observed differences in *P. maniculatus* populations indicated survival was most important in explaining variation in population size. There was some evidence for movement playing a role, but movement was not significantly correlated with the *P. maniculatus* response whereas survival was (Fig. 6), and the actual number of mice moving across the treatment boundary was quite low (only 4% of individuals were observed moving between controls and treatments). We found no indication for recruitment influencing the observed variation in mouse populations. Thus, decreased survival of mice appeared to be the key factor driving reductions in *P. maniculatus* populations following removal of the *Urophora* food subsidy. The observed differences in survival appeared strongest during winter (Fig. 5), a finding supported by other studies showing strong population-level responses in spring (Ortega et al. 2004, Pearson and Callaway 2006) and high *Urophora* consumption during winter (Pearson et al. 2000).

Drought conditions that reduced precipitation to <16% of normal during June of 2000 played a significant role in the outcome of this experiment. June is normally one of the two wettest months, and *C. maculosa* normally bolts and flowers at this time, using extensive resources. *Centaurea maculosa* declined substantially on the study area and elsewhere in western Montana at this time due to high mortality, reduced flowering, and reduced individual plant biomass (Ortega et al. 2004, Stanley 2005, Pearson and Callaway 2006). Year effects, which were likely driven by precipitation, were important in all survival and movement models (Table 1). The drought did not likely contribute substantially to the herbicide treatment, which reduced *C. maculosa* >99% on controls, since Tordon routinely causes extremely high *C. maculosa* mortality (Rice et al. 1997, Rice and Toney 1998; Y. K. Ortega and D. E. Pearson, *unpublished manuscript*). However, by reducing *C. maculosa* and therefore *Urophora* production on the control plots, the drought weakened the treatment effect by 64% almost immediately following herbicide treatment. Had the drought not occurred at this time, the *P. maniculatus* response to the treatment may have been stronger. These results suggest a bottom-up driven system where moisture inputs determine *C. maculosa* growth which in turn drives *Urophora* production, thereby influencing food resources and population dynamics of *P. maniculatus* (Pearson and Callaway 2006). They also highlight the importance of precipitation inputs in determining community interactions where water is a limiting resource (Brown et al. 2001, Fletcher and Koford 2004).

Insights regarding food limitation in natural systems

Our treatment served as a large-scale, relatively long-term experimental removal of an important food resource for *P. maniculatus*, a species which appears to be food limited (Gilbert and Krebs 1981, Taitt 1981, Morrison and Hall 1998, Yates et al. 2002). Understanding the role of food limitation in natural systems is an important field of ecological study, but 98% of work on food limitation is based on food supplementation experiments that generally offer novel food sources in unnatural spatial and temporal distributions (Boutin 1990). Thus, the novelty of food supplementation studies may limit inferences regarding how food resources in natural systems are likely to actually affect population and community dynamics (e.g., Boutin 1990, Galindo-Leal and Krebs 1998). In a seminal review on this subject, Boutin (1990) formulated two key hypotheses about the effects of food limitation in animal populations. These hypotheses were (1) animal populations should increase 1.5–2.5-fold in response to elevated food resources (originally posed by Gilbert and Krebs 1981), and (2) elevated food resources will generally increase populations but will not prevent population fluctuations. These hypotheses were derived primarily from generalizing results from food supplementation studies to develop predictions about food limitation in natural populations. To our knowledge, these predictions have not been evaluated in the context of large-scale removal of natural food sources over multiple years. The changes in abundance of *P. maniculatus* that we observed in response to removal of the *Urophora* food resource fit the first hypothesis well. The mean difference in *P. maniculatus* populations during the affected period was 1.75-fold (range 1.3–2.6-fold; Fig. 4). We also found strong support for the second hypothesis. The duration of this experiment allowed us to observe the effect of food removal on *P. maniculatus* populations over one full population period (trough to trough). Aside from the nearly twofold higher *P. maniculatus* populations on the control plots, both populations fluctuated in a remarkably consistent manner (Fig. 4). The key differences were that the increase and decline periods were much steeper and the peak much higher in the presence of the *Urophora* food resource, such that the effect of the treatment was strongest during the population high when populations approached carrying capacity. Thus, our results support the two key hypotheses proposed by Boutin (1990) regarding food limitation in animal populations based on one of the first large scale experimental removals of "natural" food resources.

In contrast, the demographic mechanisms driving the changes we observed in *P. maniculatus* populations in response to food removal differ from those drawn from food supplementation studies. From a mechanistic standpoint, the most consistent finding from food supplementation studies has been that immigration is important in determining increases in subsidized populations (Gilbert and Krebs 1981, Taitt 1981, Boutin 1990, Prevot-Julliard et al. 1999, Banks and Dickman 2000). However, most food supplementation experiments create islands of concentrated resources that can

draw in consumers from surrounding areas and are too short-term to separate the relative importance of immigration, survival, and recruitment (Boutin 1984, 1990). By estimating movement probabilities across treatment boundaries in a mark–recapture framework, we were able to evaluate the relative contribution of movement to the treatment response over 3.5 years following treatment. While food removal influenced movement, only survival was significantly correlated with *P. maniculatus* population response (Fig. 6). Thus, although there was a trend toward greater movement away from the food removal treatment and toward the food resource, movement was not significantly correlated with population size and few mice actually crossed the treatment boundary, providing little evidence for movement playing a biologically significant role in population dynamics. Our results suggest that the strong immigration responses observed in many food supplementation studies may be an experimental artifact. However, fully understanding the role of movement in animal population responses to resource fluctuations will require additional large-scale manipulations of natural food sources.

Regarding reproduction, food supplementation studies provide more variable results but commonly show an increase in reproduction or an increase in the allocation of resources toward reproduction (Boutin 1990, Schweiger and Boutin 1995, Galindo-Leal and Krebs 1998, Banks and Dickman 2000, Diaz and Alonso 2003). We found no evidence that removing a major food resource changed reproduction or allocation of energy toward reproductive output. Although the *Urophora* food resource disappears annually during the peak of the breeding season from June through August, carryover effects on reproduction are possible. Supplemental feeding studies show that energy from winter food additions can be allocated to increased reproductive output during the breeding season (e.g., Schweiger and Boutin 1995, Diaz and Alonso 2003). Nonetheless, we saw no indication of changes in body mass, sex ratios, proportions of reproductively active males or females, proportions of pregnant females, or juvenile recruitment rates in response to food removal. However, these results may be specific to our study system where the food removed was primarily a winter resource that more strongly affected survival than reproduction.

Conclusions

Exotic organisms are known to significantly impact invaded communities through competition and predation (Sax et al. 2005), but our results suggest that exotic species can also become substantial naturalized food resources for native consumers. Recent studies suggest that such exotic food resources may have significant indirect effects on other organisms within the invaded community (Roemer et al. 2001, Pearson and Callaway 2003, 2006, Noonburg and Byers 2005). Consumer interactions are an important, but poorly recognized, aspect of the invasibility and impact of exotic species, offering valuable insights for invasion, population, and community ecology (Rodriguez 2006, White et al. 2006). Understanding these interactions is also critical for effective management of invasive species. In our system, we used knowledge of native-exotic consumer interactions to mitigate exotic impacts by applying a broadleaf herbicide that restored native *P. maniculatus* populations by reducing densities of exotic *C. maculosa* and *Urophora*. The reduction in *P. maniculatus* populations to normal levels should in turn reduce indirect effects arising from elevated *P. maniculatus* populations such as increased levels of Sin Nombre virus, which appear to be primarily density-driven phenomena (Pearson and Callaway 2006). These results suggest that broadleaf herbicides may be an effective tool for managing invasive species in this system. However, we note that suppressing *C. maculosa* and restoring *P. maniculatus* populations are relatively specific goals that ignore potential treatment side effects that might impact other components of the system. For example, we observed strong increases in another exotic weed, cheatgrass (*Bromus tectorum*), in locations where it was present prior to spraying, a treatment side-effect that could present serious problems (Y. K. Ortega and D. E. Pearson, *unpublished manuscript*). Thus, even though broadleaf herbicide both reduced the target weed and restored native *P. maniculatus* populations, the tool may still have important side effects that must be weighed in the context of the specified management objectives. Improving management of invasives will require thorough understandings of management tools and how they affect native-exotic interactions.

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